

An Anthropogenetic Study on the Oromo and Amhara of Central Ethiopia

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ABSTRACT Blood samples from members of the Oromo and Amhara ethnic groups of central Ethiopia were tested for 10 erythrocyte protein systems: ACP1, ADA, AK1, CA2, ESD, G6PD, GLO1, HB β , PGD, and PGM1. Differences between the two samples were relatively slight and not statistically significant. Gene frequency distributions were then analyzed in the context of the genetics of the African and Arabian peoples. Considering the erythrocyte enzyme data, the Oromo and Amhara appear quite similar to Europoids (particularly to the South Arabians) and considerably different from the Negritic peoples. There is evidence for close genetic affinity among the Cushitic- and Semitic-speaking population groups of the Horn. Admixture between Europoid and Negritic populations seems to have been the main microevolutionary factor in generating the present day Cushitic (and Semitic)-speaking group of eastern Africa. The results are consistent with the hypothesis, supported by historical and linguistic evidence, for a common origin of these groups from a Cushitic-speaking group living in eastern Africa.

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Ethiopia is inhabited by peoples who are quite heterogeneous both culturally and biologically. Such diversity is the result of a complex network of large-scale migrations, demic expansions and contractions, and different cultural and biological interactions that occurred in prehistoric and historic times.

It has been suggested that the Paleolithic inhabitants of the country were hunters and gatherers belonging to the Khoisanoid and Europoid (Cushitic-speaking) peoples. The latter ultimately spread over the entire area of the Horn. It has also been hypothesized that Negritic tribes, the pre-Nilotes, successively (but before the third millennium B.C.) penetrated the Ethiopian plateau from the West, bringing with them the Sudanic agricultural complex. They displaced or absorbed the earlier peoples settled in the western fringes of the highlands. These migrations led also to extensive admixture with the Europoid peoples (Murdock, 1959). Other scholars have regarded the Europoid Cushitic-speaking populations and Negritic

groups as the aboriginal hunters and gatherers of Ethiopia (Clark, 1980).

Unfortunately, very little is known about the prehistory of Ethiopia. Archeological data are scanty, and the few and fragmentary remains do not indicate a great deal about the peopling and human evolution of this area. Two distinct tool-making cultures existed in the Horn of Africa during the late Paleolithic, one specialized in small stone bladelets and the other in long obsidian blades. However, the identity of the populations associated with such industries remains unclear. One point emerging from the archeological record is the absence of skeletal evidence for the presence of Khoisanoid populations in the whole of Eastern Africa (Brauer, 1978; Rightmire, 1984).

At present, Eastern Cushitic-speaking

Received May 17, 1995; accepted December 6, 1995.

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peoples are spread over vast areas of the country; they are also believed to represent the *substratum* upon which the Semitic-speaking Arabian immigrants and their derived tribes placed themselves. Their morphological and morphometric features are predominantly Europoid, but the occurrence of several tegumentary characters indicate that a certain degree of admixture with Negritic people occurred (Biasutti, 1967). The few studies on the genetic structure of the Ethiopian populations seem to support such a view (Mourant et al., 1976a; Scacchi et al., 1994). The Nilo-Saharan-speaking tribes, who are the only representatives of the Negritic people in the Country, are confined to marginal territories, scattered in the lowlands along the Ethiopian-Sudanese border.

In spite of its considerable interest, the genetics of Ethiopian peoples and their affinities are far from satisfactorily known. Not only is knowledge of the distribution of "classical" genetic markers in these populations limited, but the available gene frequency data often refer to aspecific samples (i.e., "Ethiopians," "Hamito-Semitic," "Nilotic," etc.) which have been primarily collected for medical or epidemiological studies and, therefore, are not adequate for anthropological investigations. At present, with the exception of the Amhara and the Falasha, genetic data on Ethiopian populations are essentially limited to some blood group and serum protein systems (Steinberg, 1973; Spees et al., 1975; Mourant et al., 1976b; Tills et al., 1983; Peters et al., 1986; Scacchi et al., 1994).

To help fill these gaps, a genetic survey on the Oromo and Amhara groups living in central Ethiopia (Arssi region) was done (Fig. 1). The data concern 9 erythrocyte enzyme systems, acid phosphatase 1 (ACP1), adenosine deaminase (ADA), adenylate kinase 1 (AK1), carbonic anhydrase II (CA2), esterase D (ESD), glucose 6 phosphate dehydrogenase (G6PD), glyoxalase I (GLO1), phosphoglucosyltransferase 1 (PGM1) and phosphogluconate dehydrogenase (PGD), and hemoglobin (Hb β). The genetic make-up of the two groups is also analyzed with reference to the genetics of the populations living on the African continent and the Arabian peninsula.

POPULATIONS AND SAMPLES

The Amhara are the culturally and politically dominant tribe of Ethiopia. They speak

Amharic (or Amharinya), a language belonging to the Semitic group of the Afro-Asiatic family (Ruhlen, 1987), which derived from a tongue introduced by an ancient migration of peoples from southwestern Arabia, probably during the first half of the first millennium B.C. These Arabian tribes attained cultural and political domination over the less-organized native Cushitic tribes, the Agaw, and established the old Axumite Kingdom (first to the seventh century A.D.; Kaplan et al., 1971; Ullendorff, 1973; Shack, 1974). Amhara expansion started at the end of the 13th century and was accomplished largely through the assimilation of the southern Cushitic people. Presently, they live in large areas of central Ethiopia (Fig. 1), particularly in the highlands of the Begemdir, Gojjam, Shoa, and Wello regions. The traditional rural settlement pattern consists of scattered semi-isolated homesteads, housing a few closely related families. However, villages are common near market towns or urban centers. They are an agricultural people, growing primarily grain crops (*teff*, barley, sorghum, white millet, maize, and wheat) and legumes (peas, beans, and lentils); they also keep herds of cattle, sheep, and goats. Their religion is Monophysite Christianity (the official religion of the Aksumite Kingdom since the fourth century A.D.; Biasutti, 1967; Kaplan et al., 1971; Levine, 1974; Shack, 1974).

The Oromo, also known as Galla, are the largest ethnic group in Ethiopia. They are divided into about 200 closely related tribes who speak similar dialects of the same language, Oromo or Orominya, of the Cushitic group of the Afro-Asiatic family. It is supposed that they settled originally inland on the tip of the Horn of Africa, and that, during the 12th century A.D., they migrated toward southwestern Somalia because of the expansion of the Somali tribes. Their penetration into Ethiopia occurred in the 16th century, and, at present, they are spread over nearly half of Ethiopia (Fig. 1; Grottanelli, 1955; Murdock, 1959; Huntingford, 1969; Kaplan et al., 1971). Although linguistically homogeneous, the Oromo tribes differ considerably in religious beliefs, economy, and political and social organization. Originally a nomadic people with a pastoral economy, the majority of the tribes have gradually adopted agriculture and a sedentary way of life. Today, the pastoral economy is best preserved among the Borana tribes of southern

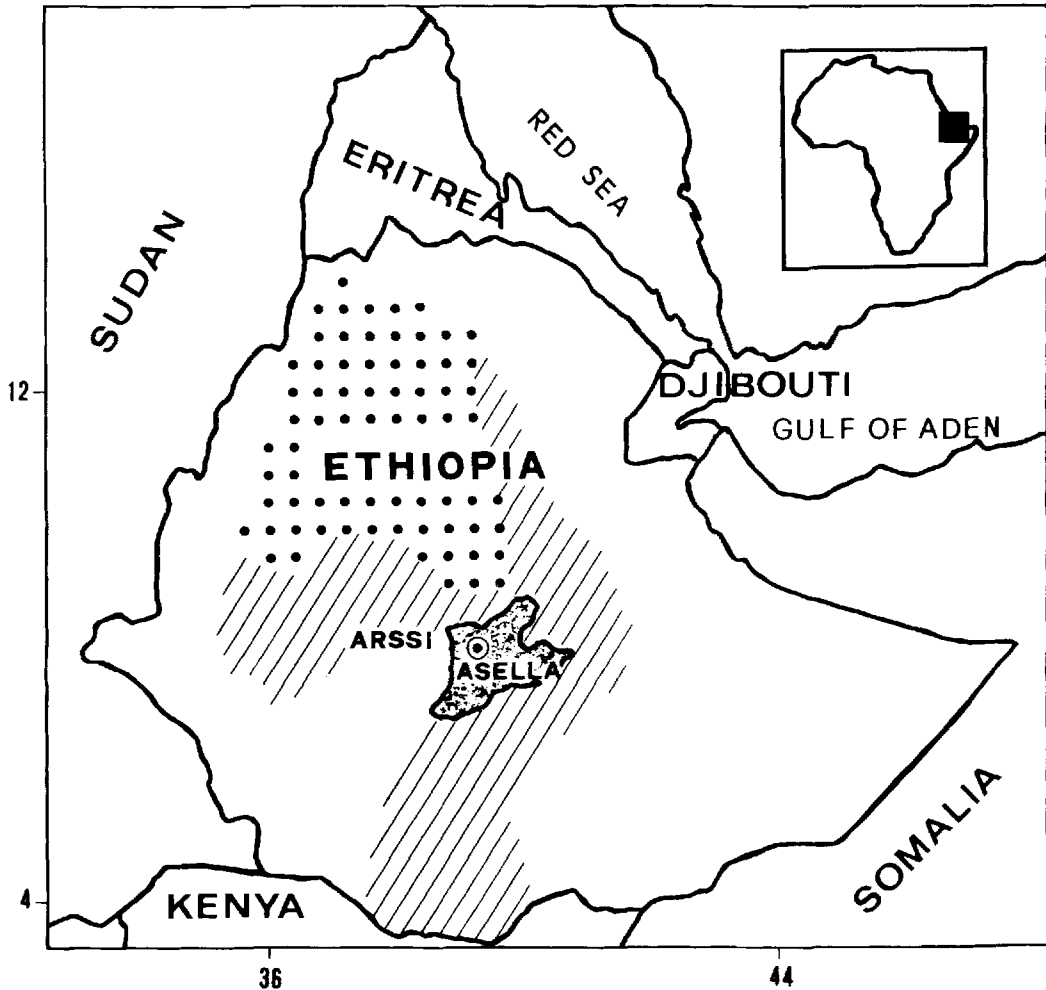


Fig. 1. Map of Ethiopia showing the Arssi province (the sampling area) and the areas where the Oromo (ruled area) and the Amhara (dotted area) live.

Ethiopia and northern Kenya, which most closely reflect the pre-16th century Oromo livelihood. Because of the Muslim influence, the majority of Oromo people have adopted Islam; Christians are limited only among those communities residing in close contact with Amhara; only a few tribes have maintained their original pagan cults (Biasutti, 1967; Kaplan et al., 1971; Lewis, 1976).

According to the latest regional census (Population and Housing Census 1984, Analytical Report on the Arssi Region, 1988), Arssi had a population of about 1,650,000 individuals, the majority living in rural ar-

reas (92%). The Arssi population is predominantly Oromo (77%) and the Amhara do not exceed 18%. However, in urban areas the Amhara and the Oromo are almost evenly distributed, accounting for 43% and 42% of the population, respectively.

The two samples consist of 81 and 86 unrelated and apparently healthy children of both sexes, with both parents belonging to the Oromo and Amhara ethnic groups, respectively. Blood specimens were drawn in Asella, the capital town of the region, and in some neighboring villages during August 1991. Blood specimens were put into sterile

tubes containing ACD as anticoagulant and kept at 4°C until sent to Rome within a few days. After three washes with cold isotonic solution (phosphate-buffered saline [PBS]), red cell samples were stored at -80°C until analyzed.

METHODS

Electrophoretic typings were performed on cellulose acetate strips (Cellogel, Chemetron Labometrics, Milan, Italy) according to the methods described by Harris and Hopkinson (1976), modified by Chemetron Labometrics for ACP1, ADA, ESD, and PGD; by Spielmann and Kühnl (1982) for AK1; by Noppinger and Morrison (1981) for CA2; by Meera Khan and Doppert (1976) for GLO1; by Betke et al. (1967) for G6PD. HB β was typed together with G6PD, and PGM1 subtypes were determined by isoelectric focusing on thin-layer polyacrylamide gel according to Kühnl and Spielmann (1978) with minor modifications.

Oromo and Amhara genetic affinities to the other African populations and to those living in the Arabian peninsula were examined by correspondence analysis (Benzécri, 1973; Greenacre and Degos, 1977; Greenacre, 1984; Lebart et al., 1984), using the NTSYS-pc package (Rohlf, 1988). Allele and haplotype frequencies were stored in the database as published in the original papers. Frequency estimates obtained from independent studies on the same population were pooled, weighted by sample size. Database and relative bibliographic sources are listed in the Appendix.

RESULTS AND DISCUSSION

Phenotype and allele frequencies are presented in Table 1. With the exception of the ESD system in the Amhara sample, none of the systems for which Hardy-Weinberg equilibrium condition was verifiable showed any statistically significant deviations between observed and expected phenotype frequencies. On the whole, differences in gene frequencies between the two samples appeared relatively slight and of no statistical significance.

Among the systems investigated, the available frequency data on the Oromo are limited only to the HB β and G6PD systems (Livingstone, 1985). The Amhara have been more extensively studied, and gene frequencies are available for ACP1, AK1, PGD, PGM1 (but not the subtypes), HB β , and

G6PD markers (Harrison et al., 1969; Livingstone, 1985). For both the tribes the gene frequency estimates observed in the present study are very close to those previously reported in literature (see Table 1).

The first general feature revealed by the survey is the evident genetic similarity of the tribes. This finding is worthy of note as the Oromo did not migrate into Ethiopia before the 16th century A.D., and because a significant degree of admixture with the Amhara has occurred only during the last century (Kaplan et al., 1971). In the Arssi region, intermarriage between the two tribes does occur, but to a small extent (Population and Housing Census, 1984, Analytical Report on the Arssi Region, 1988). In fact, the Amhara represent only a fraction of the total population (about 18% in 1984). They migrated to the region only during the last few decades, and have maintained their traditional religious faith (about 98%). On the other hand, most of the Oromo in the region are Muslims (about 70%) so that this profound cultural difference reinforces the ethnic and linguistic boundaries between the tribes.

The absence of consistent genetic heterogeneity between the Oromo and Amhara agrees with the picture obtained for some blood group systems (AB0, RH, MN, Bat-Miriam, 1962, Ikin and Mourant, 1962, and Harrison et al., 1969) and plasma protein polymorphisms (F13A, F13B, ORM1, AHSG, C6, C7, APOC2, Scacchi et al., 1994; GC, HP, PI, TF, Fuciarelli, personal communication). On the whole, these results suggest a common origin of these populations from a native Ethiopian Cushitic-speaking group.

A second finding is that, on the basis of the erythrocyte markers studied, Oromo and Amhara appear very close to the North African and South Arabian peoples. The ADA*2 allele attains a relatively high frequency compared with the other sub-Saharan African populations. In fact, African Black populations generally do not have ADA*2 at a polymorphic frequency (Mourant et al., 1976b; Jenkins et al., 1979; Hitzeroth et al., 1981; Tills et al., 1983; Roychoudhury and Nei, 1988; Destro-Bisol et al., 1992; Rickards and Martinez-Labarga, 1994; Biondi et al., 1996). A high frequency (about 7%) of the ADA*2 allele in "Ethiopians" was described by Peters et al. (1986) in a heterogeneous Amhara/Tigray sample of northwest Ethiopia. A polymorphic, but slightly lower,

TABLE 1. Phenotype and gene frequencies of red cell systems in the Oromo and Amhara population samples¹

	Phenotype frequencies					Gene frequencies	
	Oromo		Amhara			Oromo	Amhara
	Obs. no.	%	Obs. no.	%			
HB β							
A	81	100.0	86	100.0			
ACP1							
A	0	0.0	1	1.2	ACP1*A	0.056 $\pm$ 0.018	0.070 $\pm$ 0.019
AB	9	11.1	10	11.6			
B	72	88.9	75	87.2			
Total	81	100.0	86	100.0			
ADA							
1	67	82.7	71	82.6	ADA*2	0.086 $\pm$ 0.022	0.087 $\pm$ 0.021
21	14	17.3	15	17.4			
Total	81	100.0	86	100.0			
AK1							
1	80	98.8	84	97.7	AK1*2	0.006 $\pm$ 0.006	0.012 $\pm$ 0.008
21	1	1.2	2	2.3			
Total	81	100.0	86	100.0			
CA2							
1	81	100.0	85	98.8	CA2*2		0.006 $\pm$ 0.006
21	0	0.0	1	1.2			
Total	81	100.0	86	100.0			
ESD							
1	52	64.2	52	60.5	ESD*2	0.216 $\pm$ 0.032	0.262 $\pm$ 0.034
21	23	28.4	23	26.7			
2	6	7.4	11	12.8			
Total	81	100.0	86	100.0			
	$\chi^2 = 2.12$, d.f. = 1 0.10 < P < 0.20		$\chi^2 = 8.19$, d.f. = 1, 0.001 < P < 0.01				
GLO1							
1	8	10.5	13	17.1	GLO1*1	0.309 $\pm$ 0.037	0.382 $\pm$ 0.039
21	31	40.8	32	42.1			
2	37	48.7	31	40.8			
Total	76	100.0	76	100.0			
	$\chi^2 = 0.16$, d.f. = 1 $P \approx 0.70$		$\chi^2 = 0.88$, d.f. = 1, 0.30 < P < 0.50				
G6PD ²							
Males							
A	6	16.7	4	8.7	G6PD*A (males)	0.167 $\pm$ 0.062	0.087 $\pm$ 0.042
B	30	83.3	42	91.3			
Total	36	100.0	46	100.0			
Females							
AB	5	11.1	3	7.5	G6PD*A (whole sample)	0.056 $\pm$ 0.020	0.038 $\pm$ 0.017
B	40	88.9	37	92.5			
Total	45	100.0	40	100.0			
PGD							
A	63	77.8	67	77.9	PGD*C	0.130 $\pm$ 0.026	0.110 $\pm$ 0.024
AC	15	18.5	19	22.1			
C	3	3.7	0	0.0			
Total	81	100.0	86	100.0			
	$\chi^2 = 2.60$, d.f. = 1, 0.10 < P < 0.20		$\chi^2 = 1.34$, d.f. = 1, 0.20 < P < 0.30				
PGM1							
1A	27	33.3	32	37.6	PGM1*1A	0.580 $\pm$ 0.039	0.606 $\pm$ 0.037
1A1B	14	17.3	13	15.3	PGM1*1B	0.136 $\pm$ 0.027	0.141 $\pm$ 0.027
1B	2	2.5	3	3.5	PGM1*2A	0.247 $\pm$ 0.034	0.224 $\pm$ 0.034
1A2A	23	28.4	24	28.2	PGM1*2B	0.037 $\pm$ 0.015	0.029 $\pm$ 0.013
1A2B	3	3.7	2	2.4			
1B2A	2	2.5	2	2.4			
1B2B	2	2.5	3	3.5	PGM1*2	0.284 $\pm$ 0.035	0.253 $\pm$ 0.033
2A	7	8.6	6	7.1			
2A2B	1	1.2	0	0.0			
Total	81	100.0	85	100.0			
	$\chi^2 = 3.54$, d.f. ³ = 4, 0.30 < P < 0.50		$\chi^2 = 5.06$, d.f. ³ = 4, 0.020 < P < 0.30				

¹Gene frequency data available in literature on the Amhara concerning the systems studied in the present study: ACP1*A = 0.069 (N = 168), AK1*2 = 0.013 (N = 303), G6PD*A = 0.027, one sample was enzyme deficient (males, N = 113), G6PD*A = 0.032 (whole sample, N = 164), PGD*C = 0.135 (N = 100), PGD*C = 0.053 (N = 66), PGM1*2 = 0.298, PGM1*6 = 0.006 (N = 163) (Harrison et al., 1969). G6PD*def (enzyme deficiency) = 0.000 (N = 125), G6PD*def = 0.000 (N = 448), HB β *A = 1.000 (N = 180) (Livingstone, 1985). Gene frequency data available in literature on the Oromo concerning the systems studied in the present study: G6PD*def (enzyme deficiency) = 0.000 (N = 110), G6PD*def = 0.000 (N = 251), HB β *S = 0.005 (N = 91) (Livingstone, 1985).

²Phenotype typings on female individuals have been carried out since no deficient variants in the male samples had been found. Gene frequencies in males and females were pooled because they were not significantly different ($P \approx 0.05$ in the Oromo, $P > 0.20$ in the Amhara).

³2B2B and 1B2B phenotype classes were pooled with 2A2B because their expected frequencies were lower than 1.

ADA*2 frequency was also observed in the Falasha, the Semitic-speaking Ethiopian Jews (Bonné-Tamir et al., 1987). These estimates fall well in the range of the ADA*2 frequency distribution in Arabian populations (Al-Nassar et al., 1981; Roychoudhury and Nei, 1988).

The Amhara and Oromo resemble South Arabians also in the high PGD*C frequency, which is over 10%. The PGD*C frequency in North African populations is slightly lower, and in sub-Saharan African populations it does not generally exceed 8% (Mourant et al., 1976b; Spedini et al., 1980, 1982; Tills et al., 1983; Bayoumi et al., 1985; Bayoumi and Saha, 1987; Roychoudhury and Nei, 1988; Destro-Bisol et al., 1992; Rickards and Martinez-Labarga, 1994; Biondi et al., 1996). Not surprisingly, a high PGD*C gene frequency was described also for the Falasha (Bonné-Tamir et al., 1987) and the Amarar, a Cushitic-speaking Beja tribe of eastern Sudan (El Hassan et al., 1968).

The picture shown by the acid phosphatase locus 1 is markedly different from that generally observed in the African continent or in the Arabian peninsula; it resembles again the pattern found in the Amarar and the Falasha. In both tribes, ACP1*A is less common than in North African and Arabian populations, and neither ACP1*C, which is generally observed with polymorphic frequencies in Arabian and North African groups, nor ACP1*R, which is commonly found in sub-Saharan populations, has been found (Mourant et al., 1976b; Tills et al., 1983; Roychoudhury and Nei, 1988).

Few comparative data are available for carbonic anhydrase II and esterase D. One individual carrying the CA2*2 allele was found in the Oromo sample. Polymorphic frequencies of CA2*2 are typical of sub-Saharan populations, with frequencies ranging between 16% and 3% (Destro-Bisol et al., 1987, 1992; Roychoudhury and Nei, 1988; Rickards and Martinez-Labarga, 1994; Biondi et al., 1996). Although no data are available for North African and Arabian populations, this locus has turned out to be monomorphic in European and Near Eastern populations (Roychoudhury and Nei, 1988).

In the few investigated sub-Saharan populations, excluding the Tutsi of Rwanda and Burundi, the frequency of the ESD*2 allele does not exceed 16%, and generally ranges between 10% and 3% (Roberts and Papiha,

1978; Spedini et al., 1980, 1983; Le Gall et al., 1982; Roychoudhury and Nei, 1988; Destro-Bisol et al., 1992; Rickards and Martinez-Labarga, 1994; Biondi et al., 1996). In the Oromo and Amhara, and also in the Amhara/Tigray sample studied by Peters et al. (1986), ESD*2 attains higher frequencies, similar to those observed in North African and Arabian samples (Roychoudhury and Nei, 1988). In the Falasha, the ESD*2 allele occurs at a lower frequency (about 17%).

Gene frequencies at the GLO1 and AK1 loci fall within the range observed in sub-Saharan Africa, while both tribes exhibit peculiar gene frequencies at the PGM1 locus. As pointed out by Tartaglia and Rickards (1994), sub-Saharan African populations can be distinguished into two groups on the basis of PGM1*1A and PGM1*1B frequencies: a West-Central group (including populations living in Gambia, Liberia, Benin, Congo, and Central African Republic) and a South-Eastern one (Rwanda, Namibia, Botswana, Zimbabwe, and South Africa). The populations of the West-Central group generally show a higher frequency of PGM1*1A and lower frequencies of PGM1*1B (arithmetic mean frequencies of 0.78 vs. 0.65, and 0.05 vs. 0.17, respectively). The !Kung, a Khoisan population living in southern Africa, cannot be included in either group because of the exceptionally low frequency of PGM1*2A and the absence of PGM1*2B. The Amhara and Oromo appear to be much closer to the South-Eastern group, although their PGM1*2A frequency is considerably higher than that observed in all other sub-Saharan Black populations investigated.

In both samples, neither cases of G6PD deficiency nor carriers of the HB β *S allele or any other HB β variant were found. This is not surprising. Although about three-fourths of the Ethiopian territory can be considered malarious, nowhere rising above 2,000 meters in altitude, the majority of the inhabitants, particularly those with a sedentary way of life, such as the groups in the present survey, populate the high plateaus which are generally nonmalarious (Gebremariam, 1988). The G6PD*A frequency estimates fall within the range of variation observed for northern African and Arabian populations and are considerably lower than those generally found in sub-Saharan Africa (Mourant et al., 1976b; Tills et al., 1983; Bayoumi et al., 1985; Livingstone, 1985; Luzatto and Battistuzzi, 1985; El-Hazmi and

Warsy, 1986; Bayoumi and Saha, 1987; Roychoudhury and Nei, 1988).

To give a synthetic picture of the genetic relationships of the Oromo and Amhara to other African and South Arabian populations, correspondence analysis was applied. The set of systems utilized (ABO, MN, RH, ACP1, AK1, PGD and PGM1) was a reasonable compromise between the need to include an adequately representative sample, both of populations and markers.

Twelve African (the northern Egyptians, the northern Libyans, the Amharar, the Falasha, the Majingay and the N'Dindjo Sara tribes, the Mbugu, the Sango, the Nyaturu, the Sandawe, the Sukuma and the Hutu) and three South Arabian populations were considered. The G6PD or Hb β alleles were not included because of their well-known dependency on selective forces. The results are shown in Figure 2. The map is a two-dimensional representation of the relationships among the populations based on the information explained by the first two orthogonal eigenvectors. In order to better illustrate the relationship between geography and genetic variation, both geographic and genetic distances among populations were plotted simultaneously on the same plane after rigidly transforming the genetic coordinates (relative to the first two axes) by rotation, translation, and dilation to reach maximum congruence with the geographic coordinates (Lalouel, 1973, 1980). The genetic configuration explains more than 70% of the total *inertia*, and almost all of the populations are well represented on the plane with their pooled *relative contributions* higher than 60%.

The most evident feature is that the genetic configuration agrees with the geographical location of the populations. Neighboring populations appear to be genetically similar even if they speak languages belonging to a different family.

The presence of four rather tight clusters is apparent. The first is made up of the Negritic populations living in eastern Africa (the Hutu of Burundi, and the Sukuma and the Nyaturu of Tanzania, which speak Niger-Kordofanian languages, and the Khoisan-speaking Sandawe of Tanzania), which are differentiated by the second axis (12% of the total *inertia*) from the remaining Negritic tribes (the two Nilo-Saharan-speaking Sara tribes of Chad and Central African Republic, and the Mbugu and the Sango of Central African Republic, which speak lan-

guages of the Niger-Kordofanian family), all of central Africa, and grouped to form a second cluster. At the opposite side of the map, the cluster including the three southern Arabian populations is clearly distinguishable.

The fourth well-differentiated cluster is that of the Amhara and the Oromo which also incorporates the other two populations living in northeastern Africa, the Amharar and the Falasha. The Falasha, also known as the Ethiopian Jews or Black Jews, are an isolated group living in northern Ethiopia. Though their origin and early history remain obscure, they are believed to originate from the native Agaw peoples (the same tribes believed to have been assimilated by the migrating peoples from southwestern Arabia, and from which the Amhara are likely to derive), converted to Judaism in the third or fourth century A.D. (Kaplan et al., 1971; Ullendorff, 1973; Shack, 1974). The fact that the Falasha do not know Hebrew, but speak the same language as the Amhara (or Agaw dialects), that their culture is also substantially the same as that of the other Ethiopian peoples, and that even in the recent past conversion of non-Falasha to Judaism has been observed (Simoons, 1960), all seem to support this hypothesis. The Amharar are a Beja tribe living in the eastern coastal territory of the Sudan. Like the Oromo, they are nomadic herdsmen by tradition and speak a language belonging to the Cushitic branch. These four populations appear genetically located in an intermediate position between the cluster made up by the southern Arabians and that of the eastern Negritic tribes.

The remaining two populations, the Libyans and the Egyptians, are appreciably far from each other since the former appear to be quite close to the southern Arabians, while the latter are considerably shifted towards the sub-Saharan populations.

The markers which mostly contribute to this picture are CDe and cDe, which account for 80% of the *inertia* explained by the first eigenvector, and ACP1*A, PGD*C, ACP1*R, cDe, and ACP1*C, which are the most informative markers for the second eigenvector (see the *absolute contributions* listed in Table 2).

The graphic representation of Figure 2 suggests several interesting considerations that can be summarized as follows: The spatial genetic proximity of the Falasha and Amharar to the Oromo and Amhara strongly supports the hypothesis of a common origin

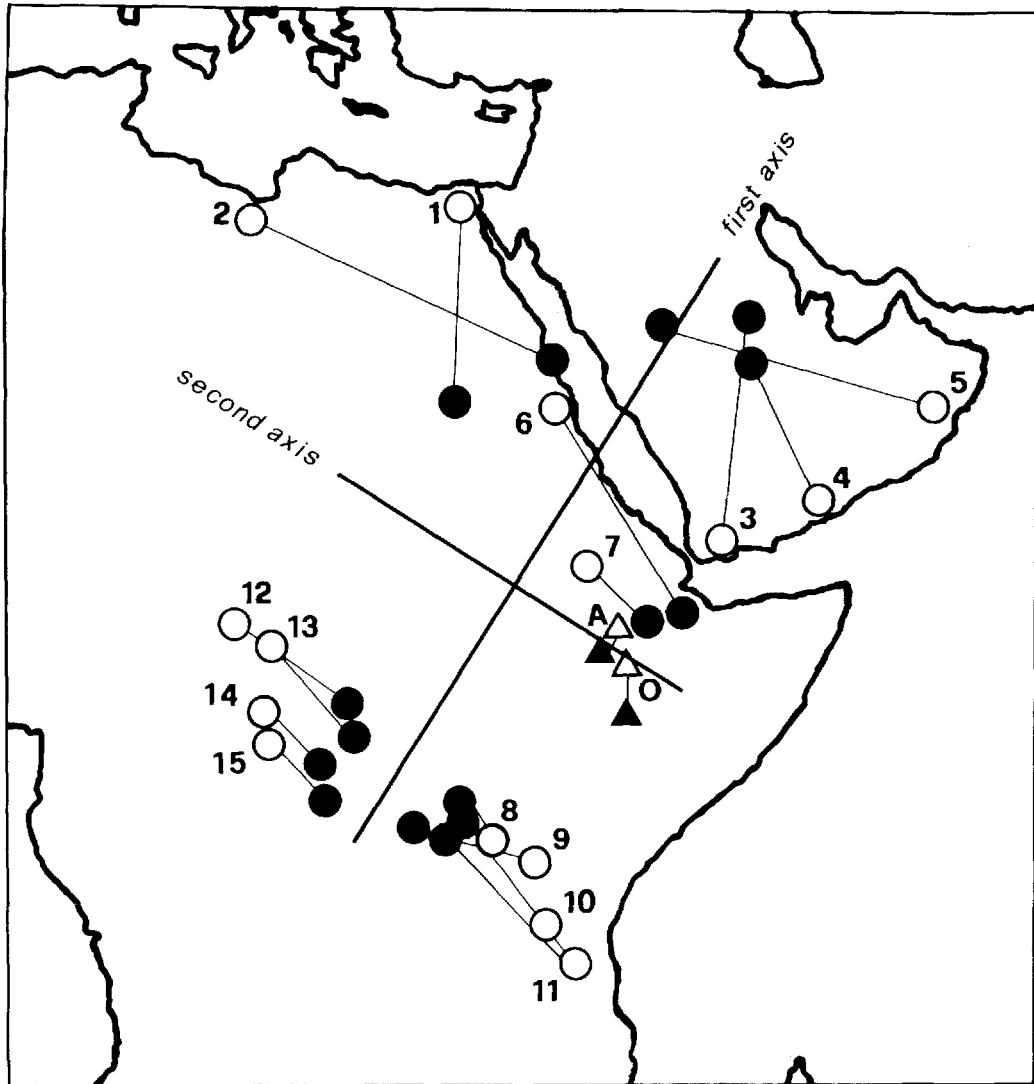


Fig. 2. Simultaneous representation of the geographic and genetic distances among 14 African (Amhara, Oromo, Falasha, Ammar, North Egyptians, North Libyans, Sara Majingay, Sara N'Dindjo, Mbugu, Sango, Hutu, Sukuma, Sandawe, and Nyaturu) and 3 South Arabian populations. The initial genetic configuration is the two-dimensional projection on the plane defined by the first two orthogonal axes (73% of the total *inertia*) resulting from correspondence analysis which includes

15 independent alleles and haplotypes at seven loci and systems (ABO, MN, RH, ACPL, AKI, PGD, and PGM1). Open symbols indicate geographic locations, solid symbols indicate genetic locations. A: Amhara; O: Oromo; 1: North Egyptians; 2: North Libyans; 3: Southwestern Arabians; 4: South Arabians; 5: Southeastern Arabians; 6: Ammar; 7: Falasha; 8: Hutu; 9: Sukuma; 10: Sandawe; 11: Nyaturu; 12: Sara Majingay; 13: Sara N'Dindjo; 14: Mbugu; 15: Sango.

of these tribes from an ancestral Cushitic-speaking group as indicated by linguistic, historical, morphological and morphometrical evidence (Biasutti, 1967; Fleming, 1976; Ehret, 1979, 1984; Brandt, 1984). The Or-

omo and Amhara, as well as the Falasha and Ammar, exhibit higher genetic affinity to the South Arabians than to the North Africans. And, by considering the projection of the populations along the first axis (61% of the total

TABLE 2. Relative and absolute contributions of the 15 independent alleles and haplotypes to the first two axes resulting from the correspondence analysis of Figure 2

Marker	Relative contributions		Absolute contributions	
	First axis	Second axis	First axis	Second axis
ABO*A	0.237	0.126	0.004	0.010
ABO*B	0.298	0.026	0.017	0.007
MN*N	0.260	0.102	0.012	0.024
CDE	0.167	0.001	0.007	0.000
CDe	0.947	0.000	0.445	0.000
Cde	0.109	0.004	0.005	0.001
cDe	0.927	0.047	0.354	0.088
cde	0.591	0.054	0.045	0.020
ACPI*A	0.016	0.693	0.002	0.347
ACPI*C	0.072	0.258	0.004	0.077
ACPI*R	0.235	0.190	0.029	0.116
AKI*2	0.393	0.009	0.015	0.002
PGD*C	0.374	0.494	0.039	0.252
PGD*R	0.114	0.005	0.004	0.001
PGM1*2	0.399	0.256	0.017	0.054

inertia), it is evident that a differential degree of admixture with Negritic peoples has characterized these populations. The major Negritic contribution is observed in the Oromo, followed in decreasing order by the Amhara, the Falasha and lastly by the Amarar. This trend agrees with the geographical location of populations.

The results also point out disagreement between information from erythrocyte enzyme data and that linked to the other "traditional" genetic markers (Mourant et al., 1976a; Excoffier et al., 1987; Scacchi et al., 1994). Erythrocyte enzyme data appear to underestimate the Negritic contribution to the Oromo and Amhara gene pools. This emphasizes again the importance of using a large number of loci and systems in the study of the biological history of human populations, since the evolution of genes does not necessarily follow the same rate and direction.

ACKNOWLEDGMENTS

We are grateful to O. Rickards, D.F. Roberts, and J.A. Peña for the stimulating discussions, and for their criticisms and suggestions on the manuscript. We thank F. Chiabrera, P. Stoppato, and L. Simonetti, members of the "Istituto per la Cooperazione Universitaria," for the help they provided during the field work. We are also indebted to G. Roro, Director of the Arssi Regional Health Department, for his help in solving logistic problems. This work was supported by 40% MURST grant allotted to G.F.D.S.

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Appendix follows

APPENDIX. Allele and haplotype frequencies utilized to study the genetic relationships of the Oromo and Amhara to other African and Arabian populations¹

Population	Ref.	ABO*A	ABO*B	MN*N	CDE	CDe	Cde	cDe	cde	ACPI*A	ACPI*C	ACPI*R	AKI*2	PGM1*2	PGD*C	PGD*R
Oromo	1	0.245	0.132	0.354	0.000	0.168	0.000	0.575	0.198	0.056	0.000	0.000	0.006	0.284	0.130	0.000
Amhara	2	0.208	0.165	0.346	0.005	0.168	0.027	0.512	0.245	0.069	0.000	0.000	0.013	0.283	0.105	0.000
N. Egyptians	3	0.260	0.147	0.604	0.005	0.325	0.011	0.186	0.336	0.246	0.035	0.000	0.024	0.248	0.038	0.000
N. Libyans	4	0.207	0.114	0.414	0.000	0.412	0.008	0.110	0.329	0.139	0.025	0.000	0.010	0.207	0.056	0.000
SW Arabians	5	0.179	0.061	0.219	0.000	0.466	0.022	0.114	0.288	0.157	0.000	0.000	0.042	0.256	0.127	0.000
S Arabians	5	0.177	0.050	0.233	0.016	0.347	0.000	0.116	0.342	0.131	0.000	0.000	0.019	0.175	0.141	0.000
SE Arabians	5	0.200	0.062	0.320	0.000	0.540	0.000	0.163	0.224	0.200	0.000	0.000	0.007	0.240	0.067	0.000
Amarar	6	0.193	0.083	0.520	0.000	0.270	0.000	0.428	0.217	0.021	0.000	0.000	0.005	0.276	0.155	0.000
Falasha	7	0.253	0.116	0.308	0.000	0.244	0.007	0.451	0.230	0.041	0.000	0.000	0.003	0.194	0.090	0.000
Sukuma	8	0.180	0.144	0.450	0.000	0.037	0.000	0.740	0.164	0.204	0.004	0.000	0.003	0.165	0.048	0.017
Hutu	9	0.192	0.119	0.474	0.000	0.079	0.000	0.750	0.140	0.124	0.014	0.002	0.006	0.186	0.049	0.002
Nyaturu	10	0.173	0.112	0.467	0.000	0.075	0.000	0.760	0.118	0.153	0.000	0.000	0.005	0.160	0.034	0.000
Sandawe	10	0.171	0.129	0.404	0.000	0.085	0.000	0.707	0.207	0.157	0.000	0.000	0.007	0.191	0.055	0.005
Sara (CAR)	11	0.179	0.285	0.479	0.000	0.120	0.000	0.622	0.155	0.124	0.000	0.064	0.000	0.182	0.031	0.000
Sara (CHAD)	12	0.113	0.144	0.422	0.000	0.035	0.019	0.533	0.269	0.246	0.003	0.012	0.000	0.186	0.005	0.000
Mbugu	13	0.190	0.111	0.488	0.000	0.042	0.000	0.687	0.229	0.223	0.000	0.043	0.019	0.075	0.034	0.000
Sango	13	0.179	0.120	0.372	0.000	0.030	0.000	0.716	0.173	0.226	0.000	0.048	0.000	0.164	0.021	0.000

¹The alleles and haplotypes that did not reach polymorphic frequencies in any of the 17 populations were not included in the analysis.

References: (1) Bat-Miriam, 1962; present study; (2) Ikin and Mourant, 1962; Harrison et al., 1969; present study; (3) Goodde et al., 1950; Mahmoud et al., 1987; (4) Kamel et al., 1975; Walter et al., 1975; (5) Marengo-Rove et al., 1974; (6) El Hassan et al., 1968; (7) Bat-Miriam, 1962; Bonné-Tamir et al., 1987; (8) Roberts and Paplha, 1978; (9) Le Gall et al., 1982; Fraser et al., 1986, cited in Roychoudhury and Nei, 1988; (10) Godber et al., 1976; (11) Jaeger, 1974, cited in Tills et al., 1983; (12) Hernaux, 1976; (13) Spedini et al., 1961, 1983.